Contributed Paper

Dynamic Conservation of Forest Genetic Resources in 33 European Countries

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Abstract: *Dynamic conservation of forest genetic resources (FGR) means maintaining the genetic diversity of trees within an evolutionary process and allowing generation turnover in the forest. We assessed the network of forests areas managed for the dynamic conservation of FGR (conservation units) across Europe (33 countries). On the basis of information available in the European Information System on FGR (EUFGIS Portal), species distribution maps, and environmental stratification of the continent, we developed ecogeographic indicators, a marginality index, and demographic indicators to assess and monitor forest conservation efforts. The pan-European network has 1967 conservation units, 2737 populations of target trees, and 86 species of target trees. We detected a poor coincidence between FGR conservation and other biodiversity conservation objectives within this network. We identified 2 complementary strategies: a species-oriented strategy in which national conservation networks are specifically designed for key target species and a site-oriented strategy in which multiple-target units include so-called secondary species conserved within a few sites. The network is highly unbalanced in terms of species representation, and 7 key target species are conserved in 60% of the conservation units. We performed specific gap analyses for 11 tree species, including assessment of ecogeographic, demographic, and genetic criteria. For each species, we identified gaps, particularly in the marginal parts of their distribution range, and found multiple redundant conservation units in other areas. The Mediterranean forests and to a lesser extent the boreal forests are underrepresented. Monitoring the conservation efficiency of each unit remains challenging; however, <2% of the conserved populations seem to be at risk of extinction. On the basis of our results, we recommend combining species-oriented and site-oriented strategies.*

Keywords: dynamic conservation, gap analysis, gene conservation unit, indicators

Conservación Dinámica de Recursos Genéticos Forestales en 33 Países Europeos

Resumen: *La conservación dinámica de recursos genéticos forestales (RGF) implica mantener la diversidad genética en el contexto de un proceso evolutivo y permitir el recambio generacional en el bosque. Evaluamos la red de áreas forestales manejadas para la conservación dinámica de RGF (unidades de conservación) en Europa (33 países). Con base en la información disponible en el Sistema Europeo de Información sobre RGF (Portal EUFGIS), mapas de distribución de especies y la estratificación ambiental del continente, desarrollamos indicadores ecogeográficos, un índice de marginalidad e indicadores demográficos para evaluar y monitorear esfuerzos de conservación de bosques. La red pan-europea tiene 1967 unidades de conservación, 2737 poblaciones de árboles y 86 especies de árboles. Detectamos poca coincidencia entre la conservación de RGF y otros objetivos de conservación en la red. Identificamos 2 estrategias complementarias: una estrategia enfocada en especies en la que específicamente se diseñan redes nacionales de conservación enfocadas a especies clave y una estrategia enfocada en sitios en la que unidades múltiples incluyen las llamadas especies secundarias conservadas en unos cuantos sitios. La red está muy desequilibrada en términos de la representación de especies, y 7 especies clave son conservadas en 60% de las unidades de conservación. Realizamos análisis de vacíos específicos para 11 especies de árboles, incluyendo evaluación de criterios ecogeográficos, demográficos y genéticos. Para cada especie, identificamos vacíos, particularmente en las partes marginales de su rango de distribución, y encontramos múltiples unidades de conservación redundantes en otras áreas. Los bosques Mediterráneos y en menor extensión los bosques boreales están insuficientemente representados. El monitoreo de la eficiencia de conservación de cada unidad sigue siendo un reto; sin embargo, <2% de las poblaciones conservadas parece estar en riesgo de extinción. Con base en nuestros resultados, recomendamos combinar estrategias enfocadas en especies con estrategias enfocadas en sitios.*

Palabras Clave: Análisis de vacíos, conservación dinámica, indicadores, unidad de conservación de genes

Introduction

The large distribution of forest trees, which commonly encompass several countries and sometimes different continents, create methodological and political challenges for conservation of forest genetic resources (FGR), especially for the development of range-wide conservation strategies and for their coordinated implementation. Because both neutral and adaptive diversity of forest trees are spatially structured at a large scale (Petit et al. 2003; Savolainen et al. 2007; Aitken et al. 2008), conservation planning, assessment, and monitoring must take place at the same scale.

A network of conservation areas should have sufficient coverage of the spatial genetic variation present in a given species. Much theoretical and applied research has been devoted to the design of conservation networks. Weitzman (1993, 1998) proposed a theoretical approach based on econometrics to define conservation priorities. Gap analysis is a widely used tool for conservation assessment and planning. In the particular case of FGR conservation, Lipow et al. (2004) applied gap analysis to examine the coincidence between protected areas and the distribution and abundance of noble fir (*Abies procera*) and Douglas fir (*Pseudotsuga menziesii*) in Oregon and Washington (U.S.A.). Hamann et al. (2004) extended this approach by estimating the local population size of 11 commercially important conifer species from inventory data and accounting for existing knowledge of their genetic diversity to define priority reserve areas in British Columbia. They used the same approach for all tree species in that province and compensated for a lack of genetic knowledge with ecogeographic data (Hamann et al. 2005). A slightly different approach was developed for Douglas fir by Coulston and Riitters (2005). They used current and predicted bioclimatic envelopes (i.e., multifactorial conditions presumably suitable for the species) to identify gaps in the distribution of protected areas.

These studies considered only the contribution of protected areas to the conservation of genetic resources. Maxted et al. (2008) extended the conceptual framework of gap analysis for the conservation of plant genetic resources and accounted for both in situ and ex situ conservation efforts. Their approach includes 4 steps: selection of target taxon and circumscription of target area, assessment of natural diversity (including genetic and ecogeographic diversity and threats), assessment of current in situ and ex situ conservation strategies, and reformulation of these strategies. Ramirez-Villegas et al. (2010) recently introduced potential distribution models into this framework.

Marshall and Brown (1975) suggest that to conserve the genetic diversity in a large area, 50 sites should be sampled to ensure including at least one copy of all common alleles with about 90% probability. However, this number of sites may not be applicable for rare species,

and it does not account for the potential diversity of local adaptations of species with large distributions (Brown & Hardner 2000). Therefore, the number of selected sites for conservation, so-called conservation units, should be determined species by species on the basis of knowledge of existing conservation units, maps of species' distributions, maps of environmental conditions (i.e., environmental zones) within each species' distribution range, and, when available, range-wide distribution of genetic diversity.

In an attempt to make gap analysis of conservation of FGR more reliable and to ensure comparability of the data among countries, European countries have agreed on common minimum requirements and data standards for the conservation units of forest trees (Koskela et al. 2012). These pan-European minimum requirements clarify the status and conservation objective of a unit, population size, management requirements, and monitoring effort. The requirements are based on the concept of dynamic conservation of genetic diversity, which aims to maintain genetic diversity over the long term while keeping evolutionary processes and adaptive potential of forest tree populations in phase with environmental conditions that may change (Ledig 1986; Eriksson et al. 1993; Namkoong 1997). Georeferenced and harmonized data on the conservation units have been collected and stored in the EUFGIS Portal (http://portal.eufgis.org/) and are based on 26 standard descriptors at the unit level (geographical area) and 18 standard descriptors at the population level (target tree species within a unit).

The conservation units entered into the EUFGIS Portal include areas where one or more tree species are designated as target species. The populations of these species are managed for long-term maintenance of their genetic diversity and are allowed to evolve in their environment (Koskela et al. 2012). The locations of conservation units are not restricted to protected areas or nature reserves; many are located in forests managed for timber production and other products or services following the conservation-through-use approach (e.g., Vivan et al. 2009). Three possible conservation objectives are recognized (Koskela et al. 2012): maintain genetic diversity in large populations (minimum population size 500 reproducing trees), conserve specific adaptations in marginal or scattered tree populations (minimum 50 reproducing trees), or conserve rare or endangered tree species in relict populations (minimum 15 reproducing trees). Currently, the EUFGIS Portal does not provide detailed forest-inventory data or genetic-diversity data on target populations.

We used data from the EUFGIS Portal to analyze the pan-European network of conservation units of forest trees. We first analyzed the regional network as a whole, considering its overall coverage of the environmental zones of the continent. We then performed specific gap analyses for a subset of 11 tree species for which

distribution maps and genetic diversity maps were, at least partly, available. We developed a set of indices to assess the network coverage in terms of countries, environmental zones, and their combination within the distribution ranges of the selected species. On the basis of our results, we devised general, continental-level FGR assessment and conservation recommendations that are applicable to other regions of the world.

Methods

Data Set Compilation and Data Quality

Forty-six countries and the European Union are signatories to FOREST EUROPE and thus are committed to conserving FGR as part of sustainable forest management. They are also committed to the implementation of the Convention on Biological Diversity. We refer to these 46 countries as Europe and considered their extent to be Pan-European.

The data set consisted of the conservation units entered into the EUFGIS database by 31 countries (Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Iceland, Ireland, Italy, Latvia, Lithuania, Luxembourg, Moldova, Netherlands, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Turkey, and Ukraine). Sweden and United Kingdom were included in the gap analysis as countries with no conservation units meeting the pan-European minimum requirements (confirmed by correspondents in the 2 countries after assessment of their existing conservation efforts).

We analyzed data in the EUFGIS Portal as of June 2011. Some of the gaps we identified may be partially covered by undocumented conservation areas or units that do not meet the minimum requirements. There are also countries that have not yet joined the EUFGIS initiative. Therefore, we did not perform a quantitative comparison among countries.

Assessment of the Conservation Network

At the network level, we evaluated the distribution of conservation units according to the area they covered, number of target species they harbored, and their forest-management objectives. We plotted all conservation units against the environmental stratification map of Europe (Metzger et al. 2005) to assess the current coverage of different environmental zones by the network.

At the species level, the allocation of designated populations to the conservation objectives (large or marginal populations, endangered species) was assessed. To identify management systems that may result in poor regeneration, we evaluated monitoring level and forest-management practices relative to the reported status of viable regeneration. We also combined the assessment of long-term viable regeneration, for which 3 categories were recognized (regeneration requiring management intervention, sporadic regeneration, and continuous regeneration), with the level of management (no intervention allowed, minimum intervention allowed, and active intervention carried out).

Species Gap Analysis

We selected 11 species for gap analysis. Silver fir (*Abies alba*), European beech (*Fagus sylvatica*), common ash (*Fraxinus excelsior*), Scots pine (*Pinus sylvestris*) and sessile oak (*Quercus petraea*) have large populations and vast distribution ranges in Europe. Brutia pine (*Pinus brutia*) and Aleppo pine (*Pinus halepensis*) are vicariant pine species with large populations distributed in the eastern and western parts of the Mediterranean basin, respectively. Black poplar (*Populus nigra*) and white elm (*Ulmus laevis*) grow in riparian forests, which are often affected by river management and agriculture. Adult wild cherry (*Prunus avium*) and wild service tree (*Sorbus torminalis*), so-called noble hardwoods, generally occur at very low densities.

During the past decade and as part of the European Forest Genetic Resources Programme (EUFORGEN), experts have compiled distribution maps of 34 tree species on the basis of existing literature and other sources. To characterize the range of environmental conditions within the current distribution of species, we compared EUFORGEN distribution maps with maps of the environmental zones of Europe (Metzger et al. 2005).

Political Indicators of Conservation Effort

To evaluate how well the 11 taxa are conserved by countries within their distribution range, we developed a simple political indicator:

$$I_P = \text{NCU/NCD},$$

where NCU is the number of countries with conservation units for the species and NCD is the total number of European countries within the distribution range of the species in the 33 countries we considered. The I_P equals 1 when all countries in the species' distribution range have established conservation units.

Environmental Indicators of Adaptive Diversity Conserved

We considered the diversity of environmental conditions within a species' distribution range as an indicator of its adaptive genetic diversity and divided the distribution maps of the species into environmental zones.

The environmental stratification for Europe (Metzger et al. 2005) has 2 levels: 13 broad-scale zones (main

ecoclimatic subregions) and 84 fine-scale strata. Because the maps of zones and distribution ranges have a similar resolution, we assumed the species effectively grow and reproduce within the zones that match with their distribution range. However, the stratum-level map is of higher resolution than the distribution maps; thus, comparing the stratum map with the distribution maps overestimates the potential range of environmental conditions where each species may be found (i.e., species do not necessarily occur in all strata identified within their distribution range). Therefore, we focused on the broad-scale zones.

We computed an environmental index as

$$I_{EZ} = NZU/NZD,$$

where NZU is the number of environmental zones with conservation units and NZD is the number of zones in the distribution range. When I_{EZ} equals 1, all environmental zones in the distribution range are represented in the network of conservation units.

We then computed a combined index that indicates the environmental diversity in the conservation network, both at the European and at national scales:

$$I_{ECZ} = NCZU/NCZD,$$

where NCZU is the number of combined country zones with conservation units for a target species and NCZD is the total number of combined country zones in the species distribution range. The I_{ECZ} equals 1 when all countries have designated conservation units in each of the environmental zones in their territory.

We derived a more quantitative indicator of environmental coverage by comparing the share of various ecological zones within each species' distribution range (measured as relative area) with the species' share of the conservation network (measured as relative occurrence within the units). Because marginal populations can represent a valuable reservoir of genetic diversity for future adaptation, we calculated the relative area of each environmental zone within each species' distribution range and defined those zones representing <5% of the range area as marginal zones. For each species, we determined how many of these marginal zones were represented in the conservation units. We evaluated the demographic risk of extinction when marginal units also had a small population size (e.g., <500 reproducing trees).

Genetic Gap Analysis

Genetic-diversity maps were available at the continental scale for 6 of the 11 species: silver fir (Ziegenhagen et al. 2005), *Fagus sylvatica* (Magri et al. 2006), common ash (Heuertz et al. 2006), Scots pine (Cheddadi et al. 2006), black poplar (Cottrell et al. 2005), and sessile oak (Petit

et al. 2002). For these species, we conducted a broad-scale genetic gap analysis by comparing the distribution of the conservation units with the species' genetic structure at the continental scale.

Results

Assessment of FGR Conservation

The 31 countries conserved 86 indigenous or naturalized European forest tree species and 6 introduced species (Supporting Information). Introduced species were also conserved following the principle of dynamic conservation of genetic diversity, but we excluded them from the analyses. The network consisted of 1967 conservation units covering a total of 218328 ha (mean unit size of 111 ha, range <1 ha to >5000 ha) and harboring 2737 populations of target species. The majority of the units were in public forests (85%). Thirteen percent were privately owned forests, and 2% were forests with other ownership arrangements.

The network covered all the environmental zones. Most of the conservation units were in the continental zone (32% of the units) and the alpine south (23%). The Mediterranean (3 zones combined) and the Boreal zones contained 14% and 3% of the units, respectively (Fig. 1).

In addition to FGR conservation, 60% of the units were also managed for multiple uses and services. Only 10% (202) of units were managed for other biodiversity-conservation objectives, whereas 49% of units were used for wood production and 42% as seed stands. Almost 13% were in forests managed for protection purposes (e.g., soil or water protection, windbreaks) (Table 1).

Conservation effort was highly variable among tree species. Seven species were conserved in >100 units each and altogether represented 60% of all units: Norway spruce (370 units), European beech (349), silver fir (227), Scots pine (207), sessile oak (195), pedonculate oak (176), and larch (125). Four species were conserved in 50–100 units, 30 species in 10–50 units, and 45 species in <10 units, whereas 15 species were conserved in only 1 unit across all of Europe.

Conservation efforts focused mainly on maintaining genetic diversity in large populations rather than conserving specific adaptations in smaller populations or relict populations of rare or endangered species (Table 1). The conserved populations were generally of larger size than the minimum required. The population size varied among species. In 23 species all conservation units included >500 reproducing trees, and in 16 species all conservation units had <500 reproducing trees.

The majority (56%) of the conserved populations was managed under the uneven-aged management system, and 9% were managed under the clearcutting and natural-regeneration management system (data not shown).
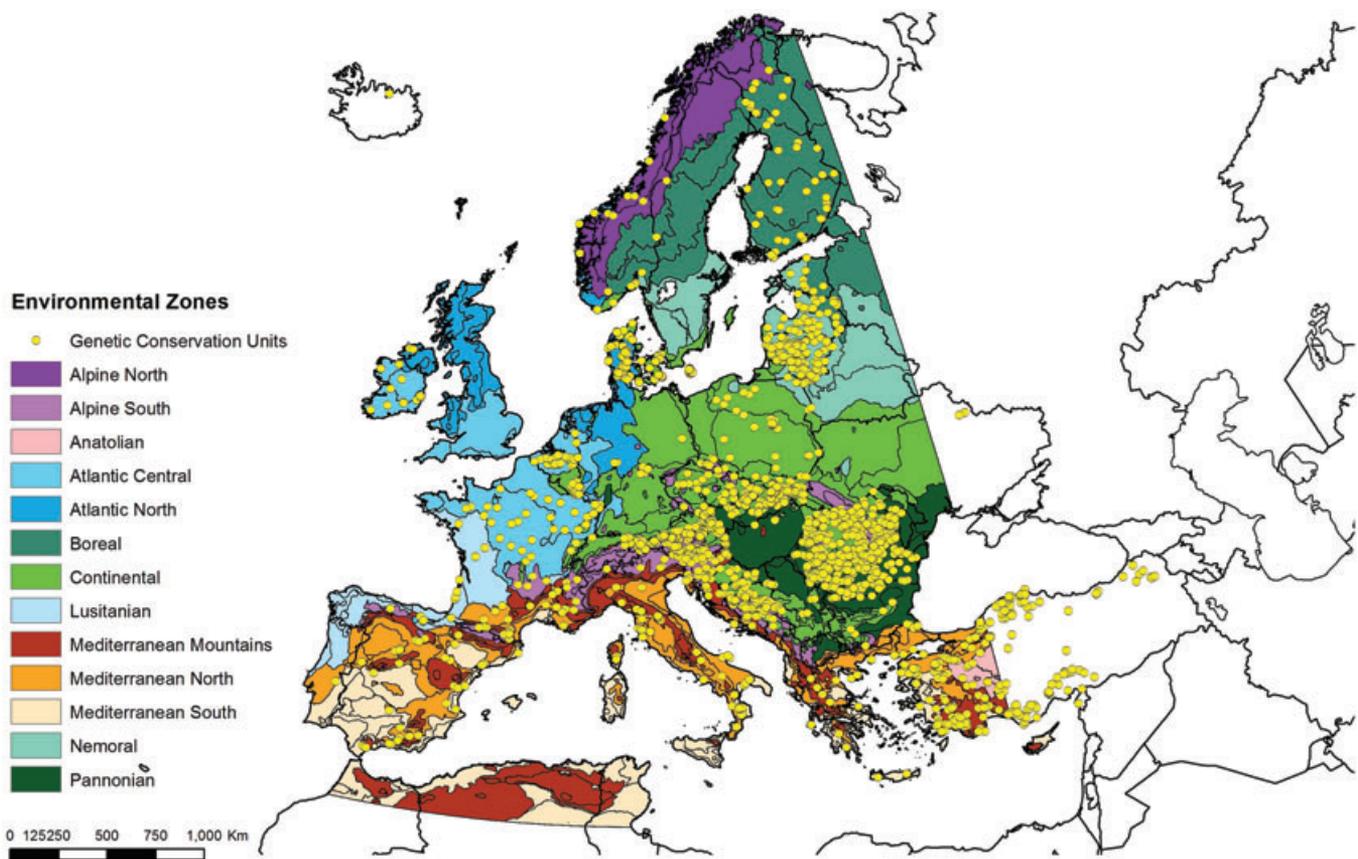
Figure 1. The 1967 conservation units of forest genetic resources in the pan-European network overlaid on a map of the 13 environmental zones of Europe (Metzger et al. 2005). The zones overlap only partially with the set of 46 European countries that actively conserve forest genetic resources.

Silvicultural intervention was prohibited in 12% of the conserved populations. In this case, the units fulfilled the minimum requirements only when natural regeneration took place without management.

Most of the conservation units (78%) included 1 target species, and 22% had >1 target species (Table 1). Two different national strategies were evident. Seventeen countries had established conservation units only for a single target species each. We named this strategy the *species-oriented strategy* because the conservation sites were chosen specifically and independently for each target species. By contrast, the remaining 14 countries designated at least one conservation unit (up to 65% of their units) for multiple target species. We refer to this strategy as the *site-oriented strategy* because the list of target species was determined for each site.

Thirty-two species were conserved by countries using the species-oriented strategy, and 83 species were conserved under the site-oriented strategy. Priority species with many conservation units were found in both groups, whereas secondary species with few conservation units appeared only in the second group.

Countries that use the species-oriented strategy generally include fewer species in their national FGR conserva-tion programs, but the 2 groups of countries had similarly distributed sizes and numbers of conservation units per target species (Supporting Information).

Forty-six percent (1266) and 66% (1818) of the target populations were surveyed within the last 5 years and 10 years respectively. For 1.3% of the conserved populations (18 out of the 1341 for which regeneration information was available), we found problematic regeneration conditions (i.e., active-management intervention necessary but not allowed). However, for some of these problematic populations, the regeneration information we used may have been outdated.

Gap Analysis

Four species with large distributions had the highest number of conservation units: European beech, silver fir, Scots pine, and sessile oak (Table 2). Although many conservation units were designated for these 4 species, the political index (I_p) indicated that 52–65% of the countries in their distribution range had designated conservation units. By contrast, there were many fewer units for wild cherry, but the proportion of contributing countries in the distribution range was similar to the previous ones.

Table 1. Characterization of 1967 forest genetic resource conservation units in Europe.

Unit (ha)	Number of units[a]
<100	1419
100–1000	474
>1000	34
no information	40
Number of target species in unit	
1	1532
>1	435
Forestry objectives in unit[b]	
wood production and multiple uses and services	969
seed stand	829
protective forest area (e.g., soil, water, timber line)	248
biodiversity conservation (habitat or species)	202
Conservation objective[c]	Number of target populations
maintain genetic diversity in large populations (minimum size 500 reproducing trees)	2163
conserve specific adaptations or phenotypic traits in marginal or scattered tree populations (minimum size 50)	427
conserve rare or endangered tree species with small or relict populations (minimum size 15)	147

[a]*Each unit includes one or several target species managed for dynamic conservation of genetic resources.*
[b]*Multiple objectives for a single conservation unit exist.*
[c]*Each target population within a unit has one conservation objective associated with it.*

Conservation of brutia pine, a species with restricted distribution range, appeared to be more complete because its I_p equalled 1 (Table 2). However, information was lacking for several countries in its distribution range that were not among the 33 participating countries or that were outside the environmental zones. Brutia pine was the only species of the 11 that had a conservation unit established outside its natural distribution range (in Italy) that was recognized as an ex situ conservation unit.

Limited conservation efforts are carried out for black poplar, wild service tree, and white elm in terms of the number of units and implementing countries. These species were also conserved in static germplasm collections.

The environmental index (I_{EZ}) was highly variable among species, ranging from 0.31 (black poplar) to 0.92 (European beech) (Table 3). In comparing index values among species, it should be kept in mind that a high en-

Table 2. Indices[a] of the pan-European conservation efforts for 11 forest tree species.

Species	NU	NCU	NCD	I_P
Abies alba	227	11	17	0.65
Fagus sylvatica	349	16	27	0.59
Fraxinus excelsior	72	15	31	0.48
Pinus brutia	60	2[b]	2	1.00
Pinus halepensis	9	4	7	0.57
Pinus sylvestris	207	14	27	0.52
Populus nigra	13	8	26	0.31
Prunus avium	46	15	29	0.52
Quercus petraea	195	18	28	0.64
Sorbus torminalis	13	9	24	0.38
Ulmus laevis	10	6	26	0.23

[a]*Abbreviations: NU, total number of conservation units in the network; NCU, number of countries with at least one conservation unit with the target species; NCD, number of countries in distribution range of the species (of 33 countries in the network); I_P, computed index value ($I_P = NCU/NCD$, $I_P < 1$ if some countries that provide data do not actively conserve the target species).*
[b]*A third country, out of the range of the species, contributes to efforts to conserve P. brutia (ex situ dynamic conservation). Data from this country are not included in the computation of the index.*

vironmental index was more easily achieved for species that were distributed in a few ecological zones, such as Mediterranean pines.

The combined index (I_{ECZ}), indicating the coverage of environmental zones within each country, was highly variable (0.07–0.75) with generally lower values than I_{EZ} (Table 3). This suggests there were considerable gaps in adaptive genetic diversity conserved within the countries.

Table 3. Indices of the environmental coverage (i.e., representation of the different environmental conditions) of the conservation network for 11 forest tree species on the basis of environmental stratification of Europe into 13 zones (Metzger et al. 2005).

Species	NZU	NZD	I_{EZ}	NCZU	NCZD	I_{ECZ}
Abies alba	7	10	0.70	28	74	0.38
Fagus sylvatica	11	12	0.92	38	116	0.33
Fraxinus excelsior	9	12	0.75	28	140	0.20
Pinus brutia	3	4	0.75	6	8	0.75
Pinus halepensis	2	5	0.40	5	24	0.21
Pinus sylvestris	10	13	0.77	33	118	0.28
Populus nigra	4	13	0.31	9	127	0.07
Prunus avium	7	13	0.54	20	129	0.16
Quercus petraea	9	13	0.69	33	128	0.26
Sorbus torminalis	4	11	0.36	9	108	0.08

[a]*Abbreviations: NZU, number of ecological zones with at least one conservation unit; NZD, total number of ecological zones in the distribution range; $I_{EZ} = NZU/NZD$, proportion of environmental zones covered in the network; NCZU, number of combined country zones with at least one conservation unit; NCZD, total number of combined country zones in the distribution range; $I_{ECZ} = NCZU/NCZD$, proportion of combined country zones covered in the network.*
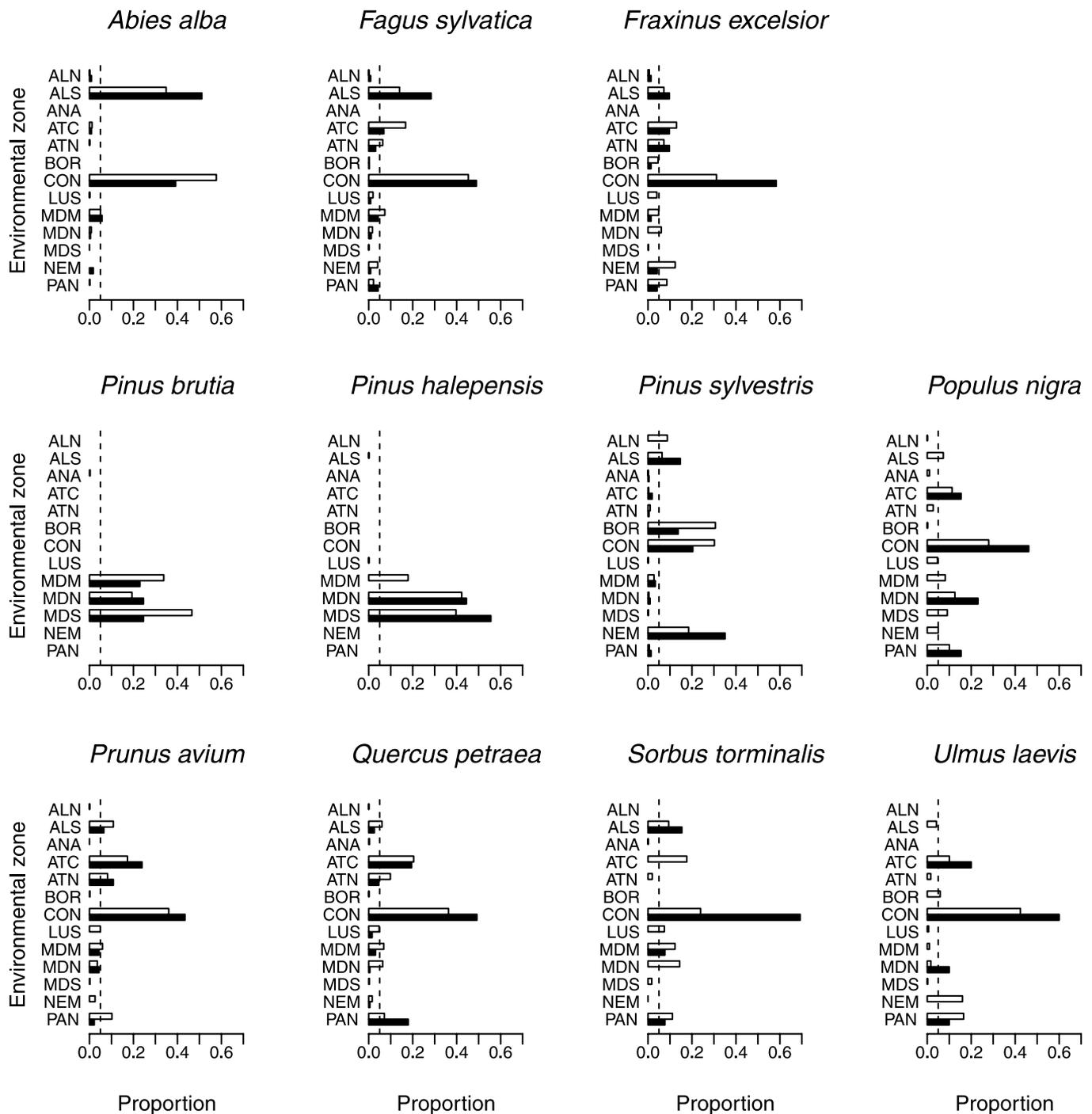
Figure 2. *Coverage of environmental zones in the conservation network for 11 tree species (white, proportion of area for each ecological zone in the distribution range of the species; black, proportion of conservation units from the network in the respective zone; vertical dotted line, 5% threshold for both variables; ALN, alpine north; ALS, alpine south; ANA, Anatolian; ATN, Atlantic north; ATC, Atlantic central; BOR, boreal; CON, continental; LUS, Lusitanian; MDM, Mediterranean mountains; MDN, Mediterranean north; MDS, Mediterranean south; NEM, nemoral; PAN, Pannonian). Level of representation of major environmental zones (i.e., representing >5% of the distribution area or >5% of the number of units) is to the right of the vertical line.*
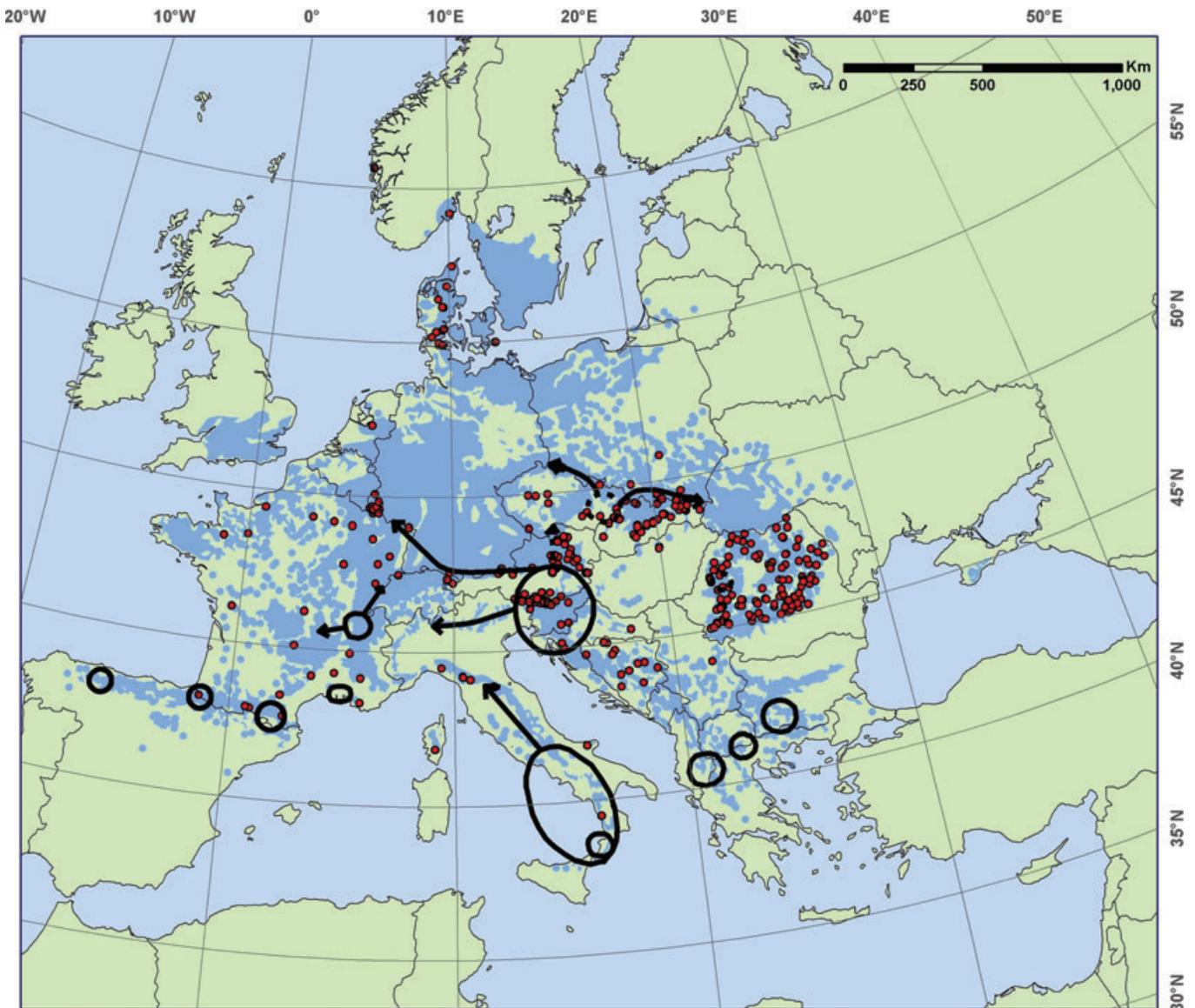
Figure 3. Coverage of glacial refugia (circles) and postglacial colonization routes (arrows) (Magri et al. 2006) by conservation units (dots) of European beech (Fagus sylvatica).

Some major environmental zones (>5% of the range area) were completely missing from the conservation network of 6 species (common ash, aleppo pine, Scots pine, black poplar, wild service tree, and white elm). Marginal zones (<5% of the range area) were missing from the network of most species (Fig. 2).

Mediterranean zones were missing from the conservation network of several species, not only for species that marginally occur in the area but also for species that have a large part of their distribution there (black poplar and wild service tree). The boreal zone was essentially missing from the conservation network for species that marginally occurred in this zone.

Some putative refugia for European beech were missing in the conservation network, in particular in the Balkan region (Fig. 3). However, the main genetic groups, as defined by Magri et al. (2006) on the basis of simple sequence repeats (SSR) and allozyme markers, were represented in the conservation network (Supporting Information).

For silver fir, mitochondrial DNA (mtDNA) diversity was structured into 2 distinct groups (Ziegenhagen et al. 2005; Liepelt et al. 2009), which were represented in the conservation network even though the southeastern mtDNA group was poorly represented. For common ash, one of the main chloroplastic DNA (cpDNA) haplotypes occurring in the western part of the distribution range (Heuertz et al. 2006) was completely missing from the conservation network. For Scots pine, 1 of the 3 lineages identified by Cheddadi et al. (2006) via mtDNA and fossil

pollen data (Italian peninsula lineage) was missing from the conservation network. For black poplar the 2 main genetic groups identified by cpDNA markers (Cottrell et al. 2005) were represented within the designated conservation units, despite their limited number. For white oaks in general (not only sessile oak), the cpDNA diversity consisted of 5 lineages that recolonized Europe and that were spatially distributed across the continent (Petit et al. 2002). Three lineages were well represented in the network (1 Atlantic and 2 continental). The westernmost part of the Atlantic lineage, however, was missing from the network. All these maps are in Supporting Information.

Conservation of FGR is often associated with other objectives in forest management. For each species, we assessed other management objectives associated with FGR conservation (Supporting Information). Conservation units of silver fir, European beech, and sessile oak were in forests managed for multiple objectives. This was also the case for common ash and Scots pine but to a lesser extent. In contrast, brutia pine conservation units were focused strictly on conservation, and aleppo pine conservation units were frequently used for seed production.

For all species, we detected very low coincidence of designated FGR conservation with other biodiversity objectives (conservation of habitats or species) (Supporting Information). The highest coincidence was found for riparian black poplar, white elm, and aleppo pine. Only 5 ecologically marginal populations, of 4 species (European beech, common ash, Scots pine, and wild cherry), had small population sizes and were at risk of extinction.

There was a general lack of information about the quality of regeneration (Fig. 4). Regeneration was sporadic in scattered and pioneer species, such as black poplar, white elm (this is also part of their biology), Scots pine, and brutia pine. We detected no difference in the regeneration quality between marginal and nonmarginal populations of the 4 above-mentioned species (data not shown).

Discussion

Our assessment of FGR dynamic conservation in Europe and the indicators we used are much more detailed compared with the genetic indicator in the FOREST EUROPE criteria and indicators for sustainable forest management (MCPFE 2003). On the basis of our results, we make the following recommendations to improve FGR conservation in Europe and believe these recommendations can be applied to other regions where genetic resources need to be conserved at a continental scale.

We recommend application of both the species-oriented and site-oriented strategies in an integrated manner in all countries: species-oriented strategy for multisite conservation of priority species (selected on the
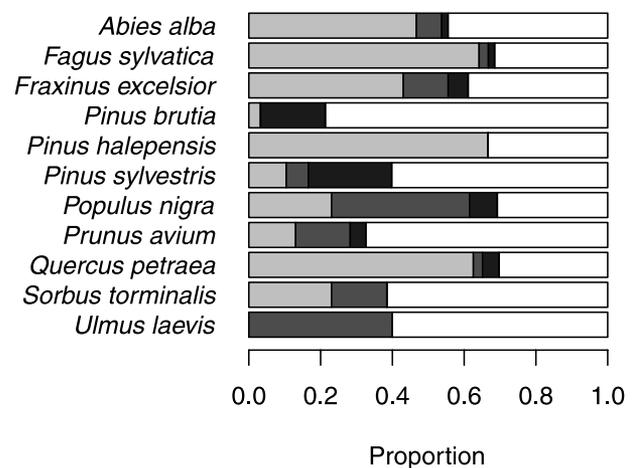

Figure 4. Cumulative proportion of the values of regeneration status in the conservation units of tree species (from light grey to black, respectively, continuous regeneration, sporadic regeneration, regeneration requiring management intervention; white, no information available).

basis of economic and ecological considerations) and site-oriented strategy to increase the number of species conserved at a continental scale. We expect that the balance between the 2 approaches will depend on the total number of target species in different regions (e.g., more emphasis on the site-oriented strategy in tropical than in temperate forests).

Conservation of FGR is achieved through various systems of forest management. For the 11 species we studied, the disconnect between FGR conservation and other biodiversity conservation systems was clear; the main exceptions were riparian species, black poplar, and white elm. Because riparian forests have high biodiversity, they have an important ecological role. Changes in their ecological dynamics also affect the population dynamics of trees and, therefore, their genetic diversity (Guilloy-Froget et al. 2002). Clearly defining continental-wide minimum requirements and data standards for conservation units, as was done in Europe (Koskela et al. 2012), would help improve the connection of FGR conservation networks with other biodiversity conservation systems and help rationalize overall conservation efforts.

The difference in the level of conservation effort carried out in Europe for different species is striking; most effort focuses on species with the highest current economic value. More generally, we recommend a minimum number of conservation units be defined at a continental scale for species that currently have low economic value but may be used in the future to diversify forest production or to maintain or restore biodiversity. Thus, FGR conservation could effectively help increase biodiversity in forests. For the most intensively conserved species, neighboring units might be genetically redundant. This

has to be checked through the use of genetic analyses. If neighboring units are genetically redundant, then reduction in the number of units would improve monitoring efficiency.

For the gap analyses, we propose 5 indices be measured for each species: total number of conservation units (NU), proportion of countries with conservation units in the distribution range (I_P), proportion of environmental zones in the distribution range covered in the conservation network (I_{EZ}), proportion of combined country zones of the distribution range covered in the network (I_{ECZ}), and conservation effort in marginal areas representing <5% of a species' distribution. These indices can be used to rationalize the number of conservation units within and among countries. They require the prior development of distribution maps for each species and maps of environmental zones at a continental scale. We believe mapping of environmental zones should receive the highest priority in other regions of the world.

In a few cases, genetic information has been used to establish conservation units (e.g., *Fagus sylvatica*). To facilitate genetic gap analyses, we recommend use of the continental network of conservation units, now well documented in the case of Europe through the EUFGIS Portal, as a reference for further studies on genetic diversity. Genetic-diversity maps may also help one evaluate the genetic effect of massive propagation and large-scale transfer of forest reproductive material on local FGR (Lefèvre 2004) and thus contribute to the debate on assisted migration (Hewitt et al. 2011). Furthermore, a representative sample of the conservation network could be used as an observatory of evolution in tree populations.

We detected a low representation of the Mediterranean environmental zones in the FGR conservation network, for both Mediterranean species and marginal Mediterranean populations of species that have a continental distribution, even though many protected areas are established in the region. We recommend increasing the FGR conservation efforts in this region, which is also a forest biodiversity hotspot (Medail & Quezel 1999; Fady-Welterlen 2005) and a reservoir of potentially interesting FGR for species' adaptation to climate change. Boreal FGR were also underrepresented and, although there are fewer tree species in this area than in the Mediterranean region, local adaptation is important there and deserves attention.

The management of individual conservation units should be improved in terms of frequency of surveys and monitoring of regeneration. Regeneration is a crucial phase in the demographic and genetic processes. Protocols for the assessment of regeneration still need to be standardized and implemented at a continental level. To produce a demographic risk indicator, we propose combining the marginality information with demographic information on the number of reproducing trees and the status of the regeneration observed over several years (depending on the normal frequency of regeneration events in the population). This demographic-risk indicator would be used to identify conservation units of high priority for intensive monitoring of regeneration and to determine whether the management system applied is compatible with the conservation objectives.

Some units may face drastic declines or unrecoverable losses of genetic diversity in the future, even though long-distance gene flow occurs in trees (Kremer et al. 2012). In such situations, demographic and genetic rescue through controlled seed or pollen transfer between neighboring conservation units may be an option to consider (Bouzat et al. 2009). Such options rely on precise information of the fine-scale spatial structure of the genetic diversity.

Acknowledgment

Supporting Information

A list of the 86 indigenous target tree species in the European network for dynamic conservation of forest genetic resources (Appendix S1), a comparison of the conservation effort among European countries with species-oriented or site-oriented conservation strategies (Appendix S2), maps of the conservation units plotted against genetic diversity maps at continental scale for 6 species (Appendix S3), and forest-management objectives other than conservation of genetic resources assigned to the conservation units of 11 species (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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